

processing (see also [16] and [17] for a related approach applied to primates). Of course, our understanding of the diagnostic information in recognition tasks will remain bound by the generative models of visual information that we can imagine — or uncover from deep convolutional neural networks, which will also require some mathematical imagination. Generative models of visual information could be the next frontier to produce information processing models of the brain and behavior.

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Vocal Communication: Decoding Sexy Songs

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Male birds communicate sexual motivation via song performance, and receiving females might eventually respond to such ‘ornaments’. A new study now shows that female zebra finches have a specialized higher order sensory (forebrain) region that preferably responds to the males’ mating songs.

Singing by male songbirds plays a major role in direct and indirect male–male competition for access to mating partners and, in consequence, is highly important for male fitness. Conversely, in many species, females chose the male mating partner (reviewed in [1,2]). Thus, a female’s mate-choice decisions are essential for her lifetime reproductive success, although it is not entirely clear what qualities she is choosing, in particular in non-territorial species. Females of certain species chose several mating partners for subsequent breeding attempts during a breeding season. Further, in some bird species, socially monogamous or not, females engage in

so-called extra-pair copulations, which might be a strategy to correct ‘wrong’ or uncertain mate-choice decisions. Although mate-choice behaviors and auditory preferences of females have been studied in a number of bird species (for review, see [1,2]), the underlying neural substrates and mechanisms are widely unknown. In a study reported in a recent issue of *Current Biology*, Van Ruijssevelt *et al.* [3] start to fill this gap. By differential mapping of neuronal activity induced by sexually versus socially salient songs they identified an area in the forebrain of female zebra finches that is particularly active upon hearing the sexually motivated singing of the male.

Zebra finches are a frequently used species to study song learning, vocal communication and the underlying neural mechanisms. Male zebra finches produce two closely related types of song, one uttered towards the female (called female-directed song) and one uttered without such specificity in varying social contexts [4]. These songs are composed of motifs, each motif being a stereotyped sequence of smaller motor units (named syllables). Female-directed songs are structurally different from undirected songs of the same singer, being more stereotyped, somewhat longer, and the syllables presented faster. While the syllables of both song types are similar



Signaling male	Receiving female's auditory regions	Decoded information	Potential functions
			
Undirected song	CMM/NCM	Identity Familiarity Novelty	Mate recognition Pair-bonding Familiarity Novelty seeking/exploration
Female-directed song	CMM/NCM	Identity Familiarity Novelty	Mate recognition Familiarity Novelty seeking/exploration
Female-directed song	Left NCC	Sexually motivated male? Sexy male?	Copulation solicitation Avoidance Reproductive tract development

Current Biology

Figure 1. Decoding of socio-sexual vocal signals.

Song-based signals are decoded by avian forebrain areas that are functionally similar to cortical association areas of mammals. While several areas including NCM (caudomedial nidopallium) and CMM (caudomedial mesopallium) respond to both undirected and female-directed male songs, females' left NCCs (caudocentral nidopallium) seem specifically active upon hearing female-directed songs, even of unfamiliar singers, in fMRI studies [3]. This NCC activity might decode 'male sexiness' or 'male sexual motivation'. NCC activity likely activates downstream neural circuits involved in the control of female courtship behaviors and reproductive system development while NCM and CMM activity might be more important for social communication and maintenance of the pair-bond.

[4,5], the vocal consistency of renditions of any particular syllable of subsequent motifs of female-directed songs is higher than such repetitions of undirected songs [5]. It should be noted that a single motif of different singers can't per se be classified as female-directed or undirected song. The production of these song types is controlled by a specialized neural circuit — the so-called song system — that shows differential activity in relation to the song type produced [5,6]. The context and its dependency on testosterone strongly suggest that female-directed songs of male zebra finches are sexual signals [4,7].

The ascending auditory system of birds projects to the forebrain area field L2, which is the equivalent of the primary auditory cortex of mammals (for review see [8]). Field L2 then distributes incoming activity to various interconnected forebrain regions [8], the complexity of these interconnected higher-order auditory and multi-sensorial regions being widely unknown. The auditory specializations of these regions, such as NCM (caudomedial nidopallium) and CMM (caudomedial mesopallium), in songbirds have been studied mainly in relation to the neural representation of songs using molecular reporters of cellular activity (i.e., immediate early gene activity) [9,10] and, in a few cases, electrophysiology [11,12]. Recently, the neural representation of natural bird

sounds in the auditory forebrain has been extended to communication calls [13]. However, these technical approaches currently allow only the study of defined target areas (electrophysiology) or suffer from area- and neuron-type-specific expression of immediate early genes, which hampers brain-wide analysis of auditory representations and the discovery of new functionally defined higher-order sensory areas.

In their recent paper, Van Ruissevelt *et al.* raised the question of whether or not female-directed song can be classified as an invariant acoustical category by a particular brain region [3]. For this, they exposed females to female-directed songs and undirected songs of unfamiliar males. Brain-wide monitoring of the responses to the playback of female-directed songs and to undirected songs was possible using fMRI of anesthetized females. Van der Linden, the senior author on the paper, pioneered the use of fMRI in songbirds such as the zebra finch over the last 10 years [14]. Surprisingly, the new study identified neural activity in a particular forebrain region, the NCC (caudocentral nidopallium) of the left hemisphere (the auditory/sensory systems are generally differentiated in both hemispheres), which was related to the hearing of female-directed song. Since these females were unfamiliar with the songs, and most likely did not memorize songs under the testing

conditions (anesthesia), the NCC seems to contain neurons (or a local circuit) that are invariant for particular high-level auditory features that characterize female-directed song [3]. Which temporal and/or spectral features the female zebra finches used to decode female-directed songs remains, unfortunately, unclear. Nevertheless, the fMRI activity was backed up with an immediate-early gene study that supported higher neuronal activity during the playback of female-directed song in the NCC [3]. Future studies of the connectivity of the NCC within the forebrain auditory complex as well as studies of the auditory properties of the NCC neurons using electrophysiology are needed to define the particular role of this brain area for decoding 'female-directed'. Other forebrain auditory regions of the females, including NCM and CMM, are also active when listening to male singers but might decode other features such as individual identity, familiarity or novelty [3,10–12] (Figure 1).

But what might be the function of decoding a male song as female-directed by the female zebra finch's NCC? Does this decode 'sexy' (Figure 1)? In this case, for mate-choice a graded neural response to female-directed songs of different males would be required [15]. However, it is unknown which acoustic features, if any, distinguish preferred mating partners from avoided ones. In particular, males combine the female-directed song with a visual courtship display — a dance towards the female [4,15]. Thus, detecting a sexually motivated male might be the first step of a female's mate choice, while visual sensory processing or audio-visual combination sensitive neurons might do the second step. Interestingly, NCC is located in a brain region that in pigeons is known as a multi-sensory region [3].

Zebra finches engage in life-long pair-bonding, which in general limits the necessity of mate choice to their first reproductive cycle [15]. Although extra-pair copulatory activities account for about 10–20% of the offspring in captivity, females need to always synchronize their sexual activity with the same male mate. Here, of course, knowledge about the males' motivation to sing, i.e. his sexual state, is important in order to coordinate the female's and the male's reproductive development. Thus, decoding 'female directed' might enhance the development

of the female reproductive tract, including follicular maturation, as suggested for budgerigars already in the 1960s [16], and induce certain behaviors like approach, nest-building or calling. Conversely, these female behaviors might further stimulate testicular development and male behaviors like calling, singing and courting.

'Good' synchrony of mates, such as coordinated exchanges of thousands of short soft calls, correlates with reproductive success [17]. Thus, the sexual valence of the decoded female-directed song depends on the connectivity of the NCC with circuits that control various pair-maintenance and courtship behaviors such as the hypothalamus and/or the dopaminergic reward system, which in turn might modify behavioral control circuits or the hypothalamus–pituitary–gonadal axis controlling the gonadal status and hormonal milieu. Since females' behavioral responses to male-directed songs increase with estrogens, NCC might respond to female-directed songs only in females with elevated estrogens. Estrogens are known to modify auditory properties of female birds' forebrain neurons [18]. Alternatively, elevated estrogen levels might be important to amplify the input of NCC to its target areas.

The identification of the NCC by Van Ruissevelt *et al.* in their recent study opens up the possibility to work out the circuit that links females' song perception to their reproductive success. In relation to this, it shall be interesting to verify if these neurons decode 'sexually motivated male' or 'sexy' in other species. A particularly good candidate for study is the canary since females respond behaviorally with a copulation-soliciting display to the hearing of the speedy presentation of particular syllables of a male [19]. Thus, the endogenous properties of the NCC might determine the structure of the males' sexual signal, the song [20].

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Sleep: Helicon Cells Charge the Circuit

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A new study in the fruit fly, *Drosophila melanogaster*, has identified a neural circuitry that connects regions that control sleep with those that encode sleep pressure. These novel cells, termed helicon cells for their unique morphology, are modulated by sleep control centers and integrate sensory information, providing a novel mechanism for gating of sleep.

Sleep is regulated by diverse environmental and physiological processes including sensory stimuli, circadian cues, and metabolic states [1].

While sleep control centers in the brain have been identified in diverse species ranging from nematodes to mammals, our understanding of how sleep gates

